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BIOLOGY.—*Embryological evidence of the evolution of man.*¹ ADOLPH
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INTRODUCTION

Our knowledge of the evolution of man is being constantly increased by contributions from four distinct fields of science which are closely coöperating. Direct evidence is furnished by paleontology, the results of which are supplemented by those of comparative anatomy. The latter study really includes embryology, since there is no distinction in principle between the finished form of an adult animal and the changes which it has undergone during growth. The fourth field comprises the investigation of individual variations, which so frequently either represent a recapitulation of ancestral conditions or foreshadow future steps in evolution; in other words, an individual, or parts of an individual, may show retardation or acceleration in comparison with the state of evolution of the species as a whole.

This paper is devoted to a brief discussion of some of the evidence, derived from embryological findings, of the evolution of the human race. While it is thus restricted chiefly to the third of the four sciences enumerated above, it will be necessary, here and there, to enter the field of comparative anatomy and also that of variations.

Few biological theories have brought about so much controversy as Haeckel's well-known biogenetic law. According to this, which today is more properly called the recapitulation theory, individual

¹ Slightly enlarged address given by the author in the symposium on *The origin and evolution of man* at the joint meeting of the Washington Academy of Sciences and the Anthropological, the Archaeological, and the Biological Society of Washington, January 20, 1925. Other papers in this symposium were given by J. C. Merriam, Carnegie Institution of Washington, and Aleš Hrdlička, U. S. National Museum. Further data on the same and closely allied subjects may be found in two other papers by the author: *Fetal growth in man*, Amer. Journ. Phys. Anthropol. 6. 1923; *Growth studies on primates bearing upon man's evolution*, Amer. Journ. Phys. Anthropol. 7. 1924.

development repeats, generally speaking, ancestral conditions; in other words, embryology in a sense corroborates paleontology. In spite of the many attacks upon this theory, the author, for one, can see ample grounds for its right to existence, but realizes also that its uncritical application in phylogenetic speculations is beset with pitfalls. This theory, which fills the rôle of a working hypothesis, should never be pressed into service where there are other more direct explanations for embryonic phenomena. There is no doubt, however, that the rudimentary, non-functioning teeth² in embryos of the so-called toothless whales can not be interpreted in any other way than by assuming that the progenitors of this animal at one time possessed teeth, not only in an early growth stage but also in adult life, where they served a definite purpose. Similarly, what other explanation could we find for the transitory appearance of gill clefts in the human embryo than the forceful conclusion that they represent a phyletic contraction, a purposeless survival of conditions of our remote past which points to one and the same stem for man and fish? Illustrations such as these, in support of the recapitulation theory, could be listed by the hundreds. They all go to show that many parts of the human body change in the course of growth in a manner resembling the successive changes which these parts have undergone during the process of evolution. This comparison of ontogeny with phylogeny—although in many respects still very hypothetical—is of the utmost value for the study of both, but for embryology particularly it furnishes explanations for phenomena which otherwise could not be understood.

Two general groups of embryological observations having a bearing upon problems of evolution can be distinguished. Into the one fall all those normal structures of a passing ontogenetic duration which can only be interpreted in the sense of atavisms. As examples may be mentioned the so-called milk lines of human embryos, indicating more than one pair of nipples in the remote ancestors of man; then the short-lived occurrence of an *os centrale* in the wrist of the human embryo, a carpal element which is present throughout life in many of the lower vertebrates. In this class belong also many of the embryonic changes in shape and relationships of the various parts of the body, such as the ontogenetic rotation of the foot or the gradual formation of the typically human promontorium on the spine, processes bearing at their beginning a striking resemblance to conditions in adult lower primates. The second group comprises all the cases

² Milk teeth as well as those of a second dentition (Kükenthal).

of closely corresponding developmental changes in different animals which prove merely some close evolutionary relationship but do not contribute, as does the first group, to a hypothetical reconstruction of ancestors.

TRUNK

Man, in the embryonic state, still possesses a true external tail, as shown, for instance, in figure 1. On the tip of this tail occurs a small appendix or so-called caudal filament which con-

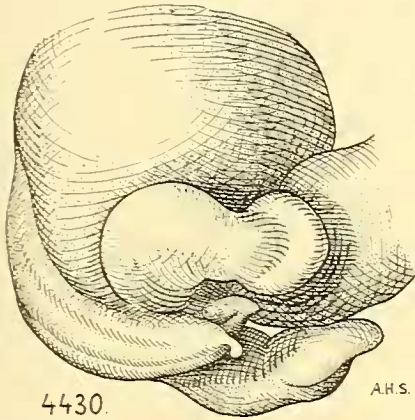


Fig. 1.—Caudal region of a human embryo (14 mm. crown-rump length) showing external tail with caudal filament.

tains no vertebral rudiments and becomes distinct when the embryo has an approximate length of 12 mm. and disappears again in embryos over 30 mm. long. Exactly the same filament is found in fetuses of many other primates, but it seems to appear later and persist longer in the tailed monkeys³ than in man. Occasionally this filament may persist throughout life. A number of such cases in man are reported in the literature;⁴ figure 2 gives an example of such a so-called soft tail,

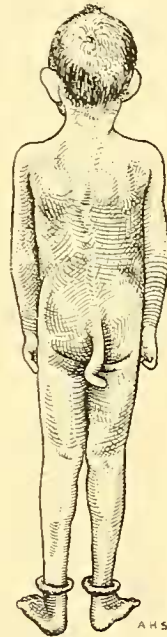


Fig. 2.—External tail, 9 inches long, in a 12-year old boy from French Indo-China (after "Scientific American," 1889, p. 296).

³ In *Cebus capucinus*, for example, the caudal filament was not yet present in an embryo of 13 mm. crown-rump length, but was well developed in one measuring 107 mm. According to Schwalbe (*Studien über Entwicklungsgeschichte der Tiere*, H. 15. Wiesbaden, 1911), a fetus of *Macacus fuscatus*, measuring 58 mm. CR., had no caudal filament as yet, whereas this structure was present in six older fetuses of the same species, ranging in size from 77 to 196 mm.

⁴ Harrison, R. G., 1901. *On the occurrence of tails in man*. Johns Hopkins Hospital Bull. 12.

Sarasin, P. 1914. *Über ein menschliches Schwänzchen*. Verhandl. d. Naturforsch. Ges., Basel 25.

which has the record length of 23 cm. This filament has also been found to persist in an adult chimpanzee and in an orang-utan, which are normally tailless, like adult man. Furthermore, the exceedingly short stump of a tail in the Barbary ape (*Inuus ecaudatus*) contains no vertebrae,⁵ and therefore in all likelihood represents an embryonic caudal filament which in this species persists in every individual throughout life.

In the human embryo the tail projects for a considerable distance beneath the level of the anus, but soon thereafter it becomes overgrown by the neighboring parts, so that it disappears from the surface and in adult life the tip of the last tail vertebra lies high above the anal level, as shown in figure 3. A still more marked reduction in a cranial direction occurs in the spinal cord, the lower end of which reaches beyond the thirty-eighth vertebral rudiment in the early embryo, but only as far as the twenty-first vertebra in the adult. In young embryos there are anywhere from 7 to 9 vertebral rudiments in the caudal region; in adult man this number has dwindled to 4 or 5 coccygeal vertebrae. Incidentally, in orang-utan this reduction in the number of tail vertebrae has gone even farther, namely, to only 3 or even 2 vertebrae. In a human embryo of 7.5 mm. crown-rump length, the tail measured 1.2 mm. in length⁶—that is, 16 per cent of the former dimension—whereas in adult man the percentage relation between corresponding measurements, i. e., the length of the row of coccygeal vertebrae and the sitting height, averages only 3.5. These data demonstrate strikingly the tremendous ontogenetic reduction of the human tail.

On the ventral side of the caudal vertebrae in the human embryo haemal processes are found,⁷ rudimentary structures which correspond unmistakably to the haemal arches or chevron bones on the proximal tail vertebrae of many monkeys. This occurrence of haemal arches in the human embryo would in itself constitute sufficient proof for a larger and well-functioning tail in our forebears; but, as shown

⁵ Waldeyer, E., 1896. *Die Caudalanhänge des Menschen*. Sitz.-Ber. K. Preuss. Akad. Wiss., phys.-math. Kl. 34.

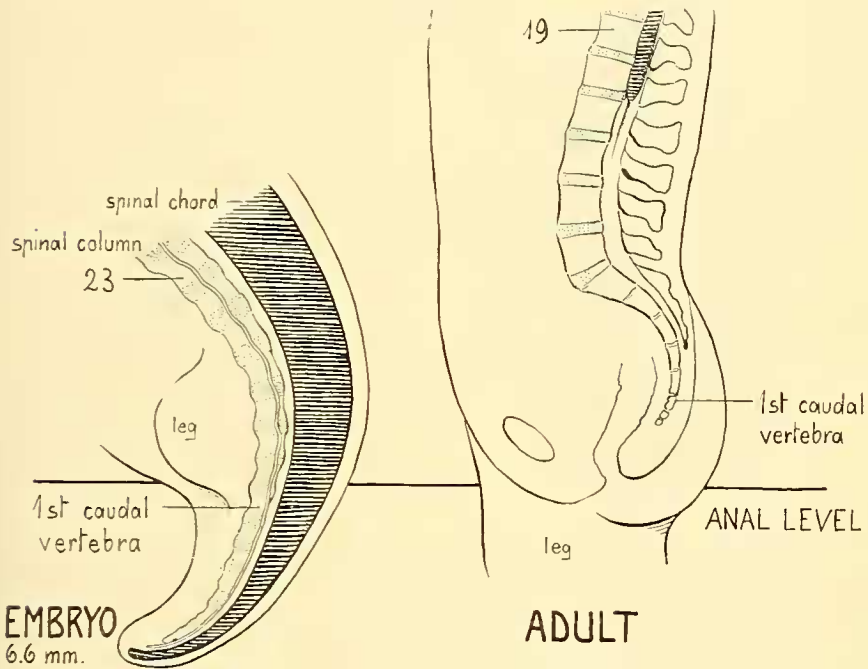
⁶ Kunitomo, K., 1918. *The development and reduction of the tail and of the caudal end of the spinal cord*. Contributions to Embryology, 11. Carnegie Inst. Washington Pub. No. 271.

⁷ v. Schumacher, S., 1906. *Über Haemalbogen bei menschlichen Embryonen*. Anat. Anz., Erg. H. 29.

Favaro, G., 1907. *Il canale ed i vasi caudali negli Amnioti, con particolare riguardo alle specie umano*. Arch. d. Anat. e di Embriol. 6.

above, embryology furnishes abundant additional proof for such a claim.

In early prenatal stages of all primates the transverse diameter of the chest is about the same as the sagittal diameter, but in the course of growth the chest becomes proportionately much broader in man and in the anthropoid apes, while just the opposite, a relative nar-



A.H.S

Fig. 3.—Diagrammatic sagittal sections through a human embryo and an adult man, showing reduction of the external embryonic tail, of the spinal column and the spinal cord. (Embryo modified after Kunitomo, Contributions to Embryology, 11. Carnegie Inst. Washington, Pub. 271, 1918.)

rowing of the chest, occurs in the monkeys and lemurs. The close correspondence in chest shape of all primates early in ontogeny and the subsequent different growth changes in the lower and higher forms, is a good example of the absence in early development of what apparently are fundamental distinctions between the different groups. The deep and narrow chest of adult lower primates and of adult quadrupeds in general is due to the action of gravity on the thoracic organs, which exerts a constant pressure downward upon the partly cartilaginous framework of ribs. In man and higher apes gravity acts in a different direction—more on the diaphragm, so that the

chest is unhampered and free to follow the broadening influence of the shoulder muscles.

Man has the lowest placed nipples of any of the primates. This extreme position is not reached, however, until growth is completed, the nipples being situated relatively higher on the trunk in the fetus than in the adult. In relation to the ribs, the nipples overlie the second intercostal space in very young fetuses, but have shifted down to the fourth or even to the fifth rib in the adult.⁸ In fetuses of monkeys and apes the nipples occupy a relative position on the

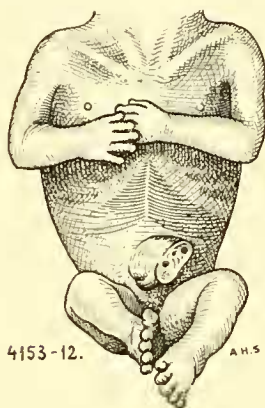


Fig. 4.—Human fetus of 10 weeks, showing the ascending clavicles (head was not drawn, since, in its natural position, it would overlap the clavicles).



NEW-CALEDONIAN

Fig. 5.—New-Caledonian man, showing the ascending clavicles in a normal position of rest. (After Sarasin, *Atlas zur Anthropologie der Neu-Caledonier und Loyalty-Insulaner*, Berlin, 1922).

trunk similar to that in human fetuses, but, in contrast to man, they shift, if at all, upward in the course of growth. From this it is justifiable to argue that both the extremely low position of the nipples in man and their exceedingly high position (close to the axillae) in such primates as the orang-utan or the howling monkey, are comparatively recent specializations, and that the common ancestors of man and other primates had nipples situated somewhere between these extremes.

In the human fetus the shoulders lie high above the suprasternal notch, so that the lateral ends of the clavicles are directed upward (fig. 4). In adult whites the collar bones, when in a normal position of rest, are almost or quite horizontally posed, but in adults of

⁸ In a fetus of the howling monkey (*Alouatta palliata*, 68 mm. CR.) the nipples overlaid the third ribs, whereas in the adult of the same species they were situated over the second intercostal space.

primitive races they have descended less from their fetal position (fig. 5). In view of the fact that in all monkeys and apes the clavicles stand very steep and do not descend during growth, it seems justifiable to conclude that the relatively low position of the shoulders in the white race is phylogenetically a progressive condition.

HEAD

In absolute size, the brain part of the head in man surpasses that of any other primate. However, if the head size is expressed in relation to the size of the trunk, man is found to stand well within

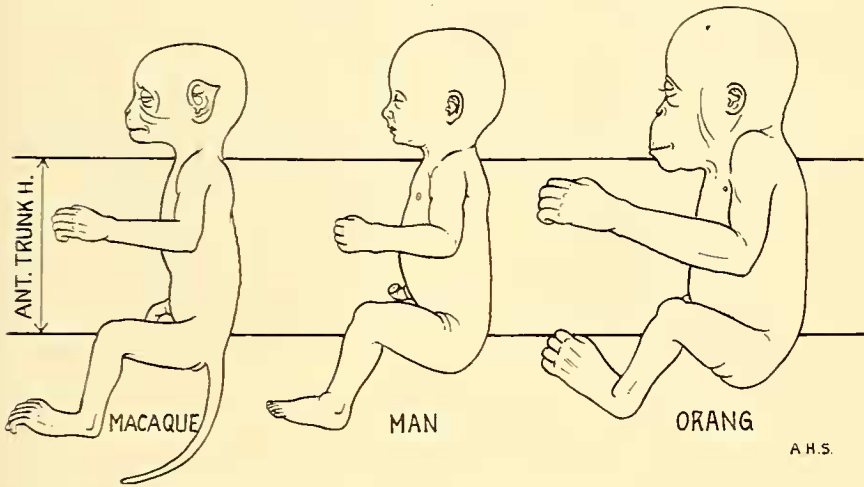


Fig. 6.—Exact body proportions in new-born macaque, man, and orang, all reduced to the same anterior trunk height.

the range of this proportion among primates, and this, too, at any stage of development. At birth, for example, as shown by figure 6, the orang has a considerably larger head than man, and in relative head size man shows little difference from the macaque. In all primates the relative size of the head, especially its brain part, diminishes with advance in growth, but it has not decreased as far in some adult monkeys as it has in adult man. The average diameter of the head (length, width, and height, divided by 3), expressed in percentage of the trunk length, amounts in man to 57 at birth and to 31 in adult life. These figures are equalled or even surpassed in many primates, the new-born gibbon and orang each having an index of 61, and among the lower forms the new-born spider monkey has an index of 56. Among adults, *Cebus apella* exceeds man by 8 units in this proportion. These figures deprive man of the distinc-

tion of having the relatively largest head, and the analogous ontogenetic process of diminishing relative head size in all primates constitutes further support for the close relationship of man, apes, and monkeys.

The eyes move relatively closer together with advance in growth, not only in man, but in all the other primates (fig. 7). Early in human fetal life the relative interocular width is as great as in adults of most other groups of animals. In approximation of the eyes, man stands at any age well within the range of variation exhibited by his simian relatives. Many of the latter⁹ have become more highly specialized in this respect than man, whose interorbital sep-

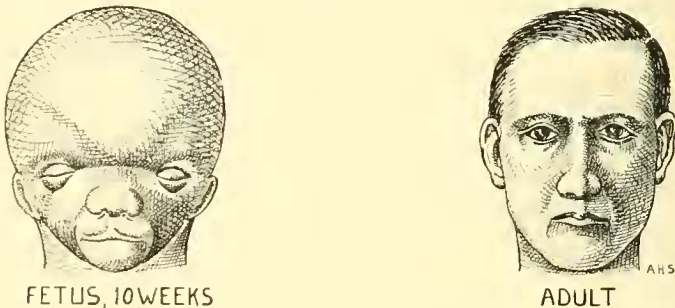


Fig. 7.—Head of a human fetus, 10 weeks old, compared with the head of an adult, showing the decrease in the relative distance between the eyes with advancing growth.

tum is comparatively broad, particularly in some of the lower races, such as the Hottentots.

The relation in size between the outer ear and the head changes in all primates with advance in growth. Generally speaking, the ear grows faster than the head, i.e., the relative size of the ear increases. In the gibbon, for instance, the index expressing this relative ear size amounts to 1.7 in a fetus of 21 mm. crown-rump length, 9.9 in a newborn, and 13.6 in an adult. In a few primates, notably those with small ears, the relative ear size, while increasing as in others during prenatal growth, decreases after birth. In man the relative ear size averages 1.3 in fetuses of 9 weeks, rises steadily to 5.9 at birth, but drops thereafter to 4.7 in adults.¹⁰ In orang-utan this

⁹ The distance between the inner angles of the eye clefts, expressed in percentage of the greatest distance between the zygomatic arches, amounts in man to 52 in fetuses of 9 weeks, to 25 in newborns, and to 23 in adults; in the orang it is 19 in the newborn, and 12 in the adult; in adult *Lasiopyga rubella* this index is 13.3, in *L. callitrichus* 15.7, in adult *Cebus capucinus* 15.1, and in *C. apella* 16.3.

¹⁰ During old age there occurs often a secondary increase in ear size, which, however, is due to a general flattening out of the ear cartilage and a decreased elasticity of the skin rather than to actual growth of the ear.

index was 2.5 in a fetus of 145 mm. length, 5.3 in an infant, and only 1.4 in an adult. This late ontogenetic decrease in relative ear size in man, orang, and probably in gorilla, i.e., in those forms which have the smallest ears among the primates (fig. 8), may be interpreted as an indication that in phylogeny, too, the outer ear of man and of these apes has independently become smaller, and is even continuing in this tendency. This view is further strengthened by the fact that the relative size and shape of the ear,¹¹ as well as the finer configuration of helix and ant-helix, are enormously variable in man. It is generally conceded that great variability characterizes

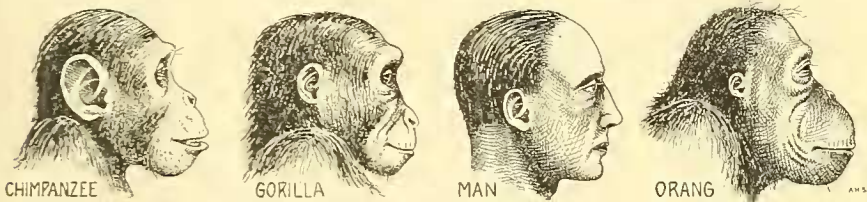


Fig. 8.—Side views of heads of anthropoid apes and man, to show the relative size of the outer ears.

such structures as are undergoing a process of reduction and have become rudimentary, as, for instance, the coccygeal vertebrae.

EXTREMITIES

The total length of the upper extremity is comparatively much shorter in adult man than in any adult anthropoid ape. This limb length, expressed in percentage of the anterior trunk height, amounts in man to 153, in chimpanzee to 180, in gorilla to 188, and in orang to 224.¹² Incidentally, there exists a greater difference in this proportion between orang and chimpanzee (44 units) than between the latter and man (27 units). In all the lower primates the relative length of the upper limb is, as a rule, markedly shorter than in man; the only exceptions to this consist in some highly specialized forms, such as the spider monkeys (*Ateles geoffroyi*, 170) and some woolly monkeys (*Lagothrix infumata*, 167). Man, therefore, occupies a conservative position in regard to his relative arm length; however, he far surpasses any other primate in relative length of his lower

¹¹ The index of the relative ear size in adult white men ranges from 3.9 to 5.8. Negroes have on an average slightly smaller ears than whites, but the ear is equally variable in the two races. The ear shape is even more variable, the morphological ear index ranging from 84 to 196 in whites and from 110 to 223 in *Aïnus* (R. Martin, *Lehrbuch der Anthropologie*, Jena, 1914).

¹² Mollison, Th. 1910. *Die Körperproportionen der Primaten*. *Morphol. Jahrb.* 42.

extremity. During individual development these different specializations in man and anthropoid apes make their appearance at quite different periods. As shown by figure 9, in apes the extreme arm length is already well defined at birth; on the other hand, the unequalled length of the lower limb, characteristic of adult man, is not even indicated at birth, since the two apes slightly surpass the human

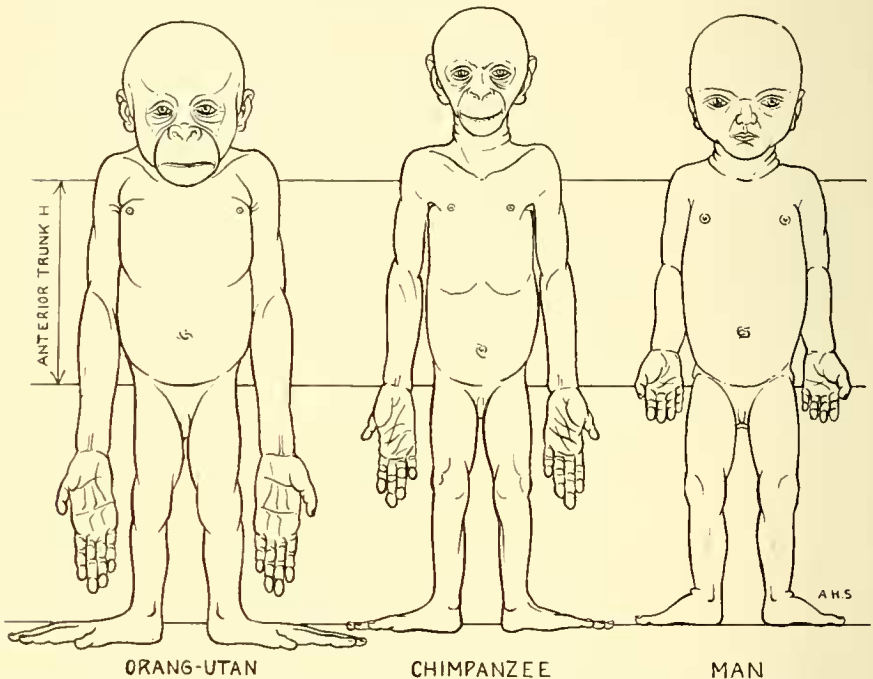


Fig. 9.—Diagrammatic representation of the exact body proportions of new-born orang, chimpanzee, and man, all reduced to the same anterior trunk height. Note the different lengths of the limbs.

newborn in length of lower limb. In view of the fact that the typical and marked lengthening in the upper extremity in apes develops so much sooner than the unique increase of lower limb length in man (fig. 10), it seems fair to assume that this human specialization is phylogenetically a later acquisition than the former characteristic of apes. This, naturally, is only a speculation, not a conclusive argument; further advance in our knowledge of growth may bring forth a different and more direct explanation or reasons for contradicting and replacing the application of the recapitulation theory.

The posterior limbs of the jumping mouse are proportionately as extremely lengthened as those of man. As in man, also, this extreme condition is not reached until late in growth, since in new-born jump-

ing mice the posterior limbs are still as short as the anterior ones. It is not to be doubted that the progenitors of these specialized rodents had shorter posterior limbs and that their ontogeny repeats their phylogeny in this respect. To be consistent, one also has to conclude that the corresponding growth change in man points to shorter legs in human ancestors.

The forearm grows faster than the upper arm, not only in man but in apes, monkeys, and lemurs. Although the relation in length between these two segments of the upper limb undergoes strikingly similar ontogenetic changes in all primates, these changes are more marked in many monkeys than they are in man. Man (particularly the white race) and gorilla have the relatively shortest forearms of all the primates. Inasmuch as the forearm is always proportionately shorter in fetuses than in adults, and since an extreme length of the forearm, exceeding that of the upper arm, is only found in late ontogenetic stages in some primates, such as the gibbon or the *Erythrocebus* monkey, it can be concluded that man and gorilla are conservative or primal in regard to this proportion, while the gibbon and others have a highly specialized forearm.

In connection with the development of the upper extremity, there exists a point of special evolutionary interest. On the ulnar side of the forearm, close to the wrist, sinus hairs occur in many (mostly arboreal) mammals. They are implanted in a more or less distinct round elevation or hillock of the skin, receive a branch of the ulnar nerve, and are regarded as touch organs. Beddard,¹³ who studied their distribution among mammals, concludes that they occur almost universally in prosimiae but are entirely missing in monkeys and apes. Since then they have been discovered in one of the primitive South American marmosets (*Hapale jacchus*) and among Old World monkeys the author found vibrissae in fetuses of the genus *Colobus*, as shown by figure 11; in the adult of this monkey no trace of either these hairs or the hillock is left. Apparently the only other primate in which this structure occurs is man, in whom the hillock alone is formed at

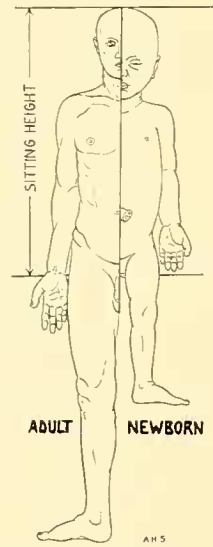


Fig. 10.—Diagrammatic comparison between the exact body proportions of adult and new-born human, both reduced to the same sitting height.

¹³ Beddard, F. E., 1902. *Observations upon the carpal vibrissae in mammals*. Proc. Zool. Soc. London 1.

an early period of prenatal development and in only a small percentage of cases (fig. 12). No sinus hairs are implanted in this hillock in man, since it develops after the embryo has reached a crown-rump length of 10 mm. and disappears again during the ninth week of fetal life; at this early age no hair could yet be expected. There can be no doubt that this rare and short-lived carpal hillock

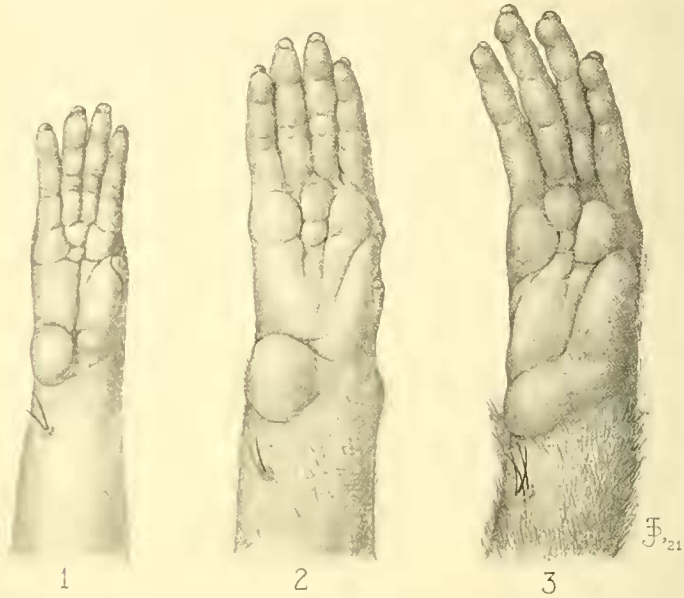


Fig. 11.—Hands of *Colobus* fetuses (1—*Colobus abyssinicus*, 112 mm. crown-rump length; 2—same species, 134 mm. CR.; 3—*C. angolensis* 147 mm. CR.), showing the rudimentary thumb and the carpal hillock and vibrissae.

in the human embryo is an atavistic structure without any possible function.

There are a number of close correspondences in the development of the hand in all primates. These, like all the previously mentioned analogies in ontogenetic processes, are claimed, on the basis of the recapitulation theory, to uphold the direct relationship between man and other primates. The hand is proportionately much broader in a fetus than in the adult, not only in man but in all the other primates as well. However, the human hand remains relatively broader throughout growth than the hand of any monkey or ape. In all primate fetuses the palmar touch pads have a very uniform arrangement, but they fade sooner and disappear more completely

in man and anthropoids than in the lower monkeys, especially those of the New World, in which they often persist well marked to adult life.

Man has a proportionately longer thumb than any monkey or ape,¹⁴ but in all primates the thumb becomes gradually shorter in relation to the hand length as growth advances. In man this ontogenetic reduction does not go so far as

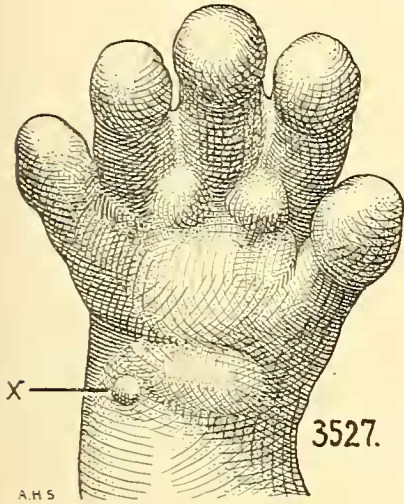


Fig. 12.—Hand of a human fetus (22mm. crown-rump length), showing the carpal hillock at X.

it does in other primates, among which the outer thumb has nearly or completely disappeared in two unrelated forms, the African *Colobus* (fig. 11) and the American *Ateles* monkey. In 56 out of 58 spider monkeys which the author recently collected, there was no trace of an outer thumb at all at any post-natal stage of growth. In one infantile (fig. 13) and one adult specimen, however, there was a well-defined, although rudi-



Fig. 13.—Hand of an infantile spider monkey (*Ateles geoffroyi*) with atavistic reappearance of a rudimentary outerthumb. Two carpal bones, the first metatarsal and the fused phalanges of the thumb, are sketched along side. Normally no trace of an outer thumb is found in these monkeys.

¹⁴ Only the baboons and some individuals among Capuchin monkeys approach closely to man in regard to the relative thumb length. In baboons this relative measurement seems to increase late in ontogeny in contrast to the growth changes in other primates.

mentary, outer thumb on the left hand only. While normally evolution has completely eliminated the thumb from the outer hand



Fig. 14.—Front view of a human fetus (25 mm. crown-rump length). The middle toe is the longest, the great toe short and abduced.

of this primate species, in individual cases a thumb may reappear as a beautiful example of atavism, which proves that the progenitor of *Ateles* once possessed a thumb. These thumbless hands must be considered as highly specialized, in direct contrast to the hand of man with its long thumb, the longest of any primate, a human distinction which is ontogenetically, and most likely phylogenetically, the most original or least changed condition. In the course of growth the attachment of the free thumb to the palm shifts proximally from its primary position at the base of the index finger. This ontogenetic migration is most pronounced in orang, somewhat less in other anthropoids and man, while in platyrrhine monkeys no such shifting takes place at all, the thumb persisting in its typically fetal position throughout life. In all primates with the exception of a large percentage of white men and perhaps some other human races, the fourth finger surpasses the second in length. In negroes this rule holds true likewise, and since the thumb is proportionately shorter and the hand narrower in the negro than in

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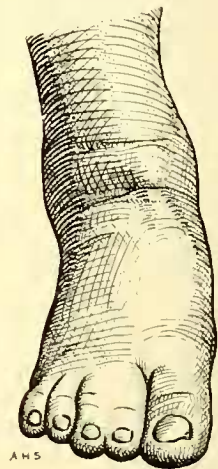


Fig. 15.—Foot of a 3-year old white boy with zygodactyly or skin fusion of second and third toes. The web in this case extends even farther than the normal webbing in the Siamang apes which derived their name (*Symphalangus syndactylus*) from this condition.

the white it can be stated that the negro has a more simian hand than the white.

In the embryonic life of all primates the soles of the feet stand nearly parallel to the sagittal body axis and thus face inward (figs. 4, 14). In the course of growth the feet rotate until the soles face downward, but in the human newborn, as well as in adult monkeys, it is still chiefly the lateral edge of the foot which is placed on the ground. This supinatorial position of the feet in the human embryo is the cause of certain conditions in the early development of the tarsus which must be regarded as primitive according to the teachings of comparative anatomy.



Fig. 16.—Feet of adult anthropoid apes and man (Orang after a specimen in the author's collection; chimpanzee after O. Schlaginhaufen, *Abhdl. u. Ber. K. Zool. u. Anthropol.-Ethnogr. Mus., Dresden*, 11. 1907; first gorilla, after R. Hartmann, *Der Gorilla*, Leipzig, 1880; second gorilla, after C. E. Akeley, *Natural History* 23. 1923). Note the differences in relative length of the toes and in the place of attachment of the great toe.

Among adult primates one finds widely different types of feet, but in young human, ape, and monkey embryos the feet are strikingly similar. At this stage of growth the great toe is considerably shorter than the second and stands much abducted in all primates.

In monkeys and apes the middle toe surpasses all the others in length, and it is interesting to note that man occasionally also conforms to this rule, although only for a very short transitory stage in his ontogeny, since in a fair percentage of fetuses at the end of the second or the beginning of the third month the middle toe is the longest (fig. 14). Very soon thereafter the second toe becomes the longest, and not until the fourth month does the great toe begin to

project farther than the others, and then only in a minority of cases. Even in adult man the great toe is shorter than the second in a considerable number of whites and in the majority of negroes. Whereas in man, therefore, the great toe becomes proportionately longer with advance in growth, in all other primates just the reverse condition prevails, namely, a gradual ontogenetic shortening of the relative hallux length.

The lateral toes (II to V) are proportionately short in all primate embryos, but, while the digits become relatively still shorter in man towards the completion of growth, they change in just the opposite sense in monkeys and apes, in which these toes are at times extremely lengthened in the adult.

In all primates the great toe is found to branch from the sole, just at the base of the second toe, in very early growth stages. This embryonic position is retained throughout life in man, whereas in all other primates the place of attachment of the great toe shifts proximally, similar to the ontogenetic shifting in the attachment of the thumb to the palm from the base of the index finger to a place nearer the wrist. In the gorilla this shifting of the hallux is least pronounced of any of the apes, whereas it is most extreme in the orang, a greater difference existing in this respect between the latter and gorilla than between gorilla and man (fig. 16). Other proportions on the foot lead to similar conclusions; in regard to the relative length of toes II and V, for instance, there exists a greater gap, as shown by figure 16, between the adult orang and gorilla (particularly *Gorilla beringeri*) than between the latter and man, and the extremely short lateral toes of man are certainly no more specialized than the exceedingly long ones of orang. Finally, if the distance from the tip of the hallux to the heel is expressed in percentage of the total foot length, an approximate relative great toe length is obtained which in adults amounts to as little as 52 in orang, to as much as 88 in gorilla, and to 100 in man, again a greater difference between two apes than between an ape and man. Data such as these are of importance in placing a proper value on some of the human specializations. We know that the great toe in man has become singularly strengthened and adduced, both phylogenetically and ontogenetically. However, fully as marked a deviation from the original type of great toe has occurred in orang, in which the hallux has become rudimentary. This assertion is further borne out by the frequent finding in this ape of a complete lack of a nail and

only one single phalanx in the great toe, symptoms of degeneracy resembling closely those occurring rather frequently in the little toe of man.

For a short time during the development of the human foot, just after the digits make their appearance on the foot plate, the toes are united by webs. This webbing between the second and third toes is slightly more extensive and disappears somewhat later than that between any of the others. A web between the second and third toes exists normally in adults of many marsupials, insectivores and prosimiae; furthermore in *Cerocebus* monkeys, in the Siamang apes, and occasionally in some gibbons. It is of great interest in this connection to find not infrequently skin fusion of the same toes in human children (fig. 15) and adults, where this condition is known to be inherited and is described under the term of syndactyly or, more recently, zygodactyly. It is normal in the embryo, persists normally throughout life in many mammals, including various primates, and occasionally persists in man, representing an atavism, not an anomaly.

CONCLUSIONS

An almost endless number of other embryological findings, bearing upon man's evolution, could be added to these scattered data which are largely the results of the author's own investigations. It is hoped, however, that the above discussion suffices to demonstrate that embryology is capable of producing valuable corroboration of evolutionary deductions from comparative anatomy and palaeontology, as well as of shedding new light on ancestral conditions of the human body.

The outstanding conclusions from these embryological studies can be summarized by stating that the many striking resemblances between man, ape, and monkey in early development, and their frequently closely corresponding growth changes can only be understood by assuming one common origin for all primates, including man, from which they inherited the tendency for the same ontogenetic processes which have become modified in many instances through a variety of later specializations. Furthermore, there exists ample evidence for the conclusion that the human body is in many points less specialized and hence has remained in some parts phylogenetically, as well as ontogenetically, more original and "primitive" than have various other primates.